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Cover Foto:
Adult siamang pair (*Hylobates syndactylus*) during a duet song bout. Both siamangs on the Foto are producing so-called boom notes. While producing these notes, the mouth is almost completely closed and the throat sac is being inflated. Notice the close proximity between the singers. Foto: Thomas Geissmann, Sept. 1998, Taman Safari Zoo, Cisarua, Java, Indonesia.

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DUET SONGS OF THE SIAMANG, *HYLOBATES SYNDACTYLUS*: I. STRUCTURE AND ORGANISATION. GEISSMANN, T.

Key Words: Duet, song, siamang, *Hylobates syndactylus*, gibbons, vocalisations

Abstract

Siamangs (*Hylobates syndactylus*) produce loud and long song bouts which are mostly exhibited by mated pairs. Typically, mates combine their partially sex-specific repertoire in relatively rigid, precisely timed and complex vocal interactions to produce well-patterned duets. This study presents a detailed description of singing behaviour, repertoire, and song and duet organisation of several adult pairs of captive siamangs. A comparison of the findings of the present study with previously published descriptions of siamang duetting behaviour reveals that various authors have been using different terms when referring to the same vocal elements, while others have applied the same names to completely different elements. In addition, the organisation of both the song bout as a whole, as well as the great call sequence in particular, is more complex than has been believed previously.

1. Introduction

The siamang gibbon (*Hylobates syndactylus*) is distributed mainly over the mountain regions of Sumatra and southern peninsular Malaysia (CHIVERS, 1977; GEISSMANN, 1995; GROVES, 1972; MARSHALL and SUGARDJITO, 1986). Like most other gibbon species (e.g. CHIVERS, 1984; LEIGHTON, 1987), the siamang lives in tropical rain forest, shows extreme adaptations for arboreal locomotion, a monogamous social structure, and exclusive use of actively defended territories by small family groups (e.g. CHIVERS, 1974; CHIVERS and RAEMAEKERS, 1980; NORIKOSHI, 1986; PALOMBIT, 1992; WEST, 1982).

RAFFLES (1821), who presented the first description of the siamang as *'Simia syndactyla'*, already noticed its spectacular vocalisations: "This new species of gibbon is abundant in the forests near Bencoolen, where they are seen in large companies, making the woods echo with their loud and peculiar cry" (RAFFLES, 1821, p. 241). As in other gibbon species, the long and loud calling bouts of the siamang follow a non-random sequence of phrases (e.g. HAIMOFF, 1984; LAMPRECHT, 1970) and are, therefore, here termed "songs", following the definitions presented by THORPE (1961) and TEMBROCK (1977) (see section 2.4).

Siamang songs are mostly exhibited by mated pairs. Typically, mates combine their partially sex-specific repertoire in relatively rigid, precisely timed and complex vocal interactions to produce well patterned duets (e.g. CHIVERS, 1974, 1978; FOX, 1977; HAIMOFF, 1981, 1983a, b, 1984; LAMPRECHT, 1970; MARSHALL and SUGARDJITO, 1986; WEST, 1982). Other members of the family group may join in the songs. Song bouts have an average duration of about 17 minutes, are mainly uttered in the early morning hours and frequently seem to elicit song bouts of neighbouring family groups (e.g. CHIVERS, 1974; GEISSMANN, 1986; MCCLURE, 1964; ORGELDINGER, 1999).

HAGEN (1890) was probably the first to describe that in the song of wild siamangs in Sumatra the various members of a family group set in at specific points of the song bout. This observation was confirmed later in wild siamangs (e.g. SELENKA and SELENKA, 1925) and in captive animals (SCHIRMEIER, 1966).

LAMPRECHT (1970) accurately described for the first time the sexual dimorphism in the vocalisations of captive siamangs. He paid special attention to a long and complex sequence of notes which he recognised as a duet. LAMPRECHT realised that a typical siamang song bout consists of an initial part (which is produced only once during a song bout), followed by an alternation of relatively rigidly organised duet parts mentioned above and more variable in-between parts ("Zwischenphasen"). These three different parts as well as the accompanying locomotor behaviour were later described and analysed in more detail by HAIMOFF (1981) who named them "introductory sequence", "great call sequence", and "organising sequence", respectively. A comprehensive description of the behaviour of wild siamangs was provided by CHIVERS (1974), and detailed descriptions of the behaviour of captive siamangs were presented by FOX (1977) and ORGELDINGER (1989, 1999).

The aims of the present study are to describe the structure and organisation of the duet song of adult siamangs, and to compare the results with previous descriptions of siamang singing behaviour.

2. Animals, Materials and Methods

2.1 Materials and Methods

In order to describe siamang song organisation, 9 adult siamangs in 10 different group constellations have been observed. The animals were kept at the Zoological Garden of Zürich (Switzerland) and at the "Zoo Seeteufel" in Studen near Biel (Switzerland). For the sake of brevity, these zoos will hereafter be referred to as Zürich and Studen, respectively. Between November 1980 and February 1985, tape-recordings of 134 song bouts were made in Zürich (n = 80) and Studen (n = 54). As a supplement, a short sound film (8 mm) of siamang duets was made in Zürich. Animals, their groupings, the number of song bouts tape-recorded of each grouping and the recording dates are listed in Table 1.

During the study, one male siamang (*Na*) was transferred from Zürich to Studen and paired up with a solitary female. One further male (*Bh*) was switched from one female to another at the Zürich Zoo. This resulted in the formation of two new pairs, one in Zürich and one in Studen (see below). The present study uses vocal data from all pair combinations.

Duration and frequency measurements of vocalisations were carried out on song bouts tape-recorded of 17 siamang groups at the following zoos: Hong Kong (China), Doué-La-Fontaine (France), Dortmund, Dresden, Frankfurt and Munich (Germany), Jakarta and Taman Safari/Cisarua (Indonesia), Studen and Zürich (Switzerland), and Howletts and Twycross (UK). Supplementary observations were carried out, and tape-recordings were made, of the siamangs at the zoos of Duisburg (Germany) and at the Metro Zoo in Miami (U.S.A.). In addition, songs of an adult hybrid female (*H. muelleri* x *H. syndactylus*) kept at the Yerkes Regional Research Primate Center (Atlanta, U.S.A.) were also recorded on tape and compared to those of pure siamangs.

Table 1: Study animals, their groupings, and the number of tape-recorded songs. Siamangs exhibiting an immature vocal repertoire are shown in paarentheses.

Animals	**Zoo**	**Study period**		**Tape-recorded song bouts**
		Begin	**End**	
Ga+*Na*	Zürich	29 Nov 1980	14 July 1981	17
Bh(+*Ch*)	Zürich	29 Nov 1980	12 Aug. 1981	23
Ga	Zürich	14 July 1981	12 Aug. 1981	4
Bh+*Ga*	Zürich	12 Aug. 1981	28 April 1982	33
(*Fa*+*Da*)+*Ch*	Zürich	12 Aug. 1981	20 Nov. 1984	2
(*Da*+)*Ch*	Zürich	20 Nov. 1984	22 Feb. 1985	1
Vr	Studen	6 July 1981	14 July 1981	10
Na+*Vr*	Studen	14 July 1981	24 Nov. 1981	34
Bb+*Ra*	Studen	6 July 1981	8 Oct. 1981	4
Ra	Studen	8 Oct. 1981	24 Nov. 1981	2
Ko+*Cr*(+*Li*+*Al*)	Studen	6 July 1981	24 Nov. 1981	4
Total				134

Most tape-recordings from siamangs kept in Swiss zoos were made with a UHER 4200 Report Stereo S and a UHER 4200 Report Stereo IC reel tape recorder (with tape speed set at 9.5 cm/s), equipped with a AKG directional microphone. All other tape-recordings were made with a Sony TC-D5M or a Sony WM-D6C tape-recorder, both equipped with a Sennheiser ME80 (+K3U) directional microphone.

Sonagrams of song sequences were made with Canary 1.2.4 software (Charif et al., 1995) on an Apple personal computer (PowerMacintosh 7600/120). Recording parameters: 11 kHz sampling rate, 16 bit sampling. Analysis parameters: FFT, Hamming analysis window; analysis resolution: 43.7 Hz filter bandwidth, 1024 points frame length; grid resolution: 23.1 ms time, 75% overlap, 5.4 Hz frequency, 2048 points FFT size. Duration and frequency measurements of vocalisations were also carried out using Canary 1.2.4 software. In addition, sonagrams of selected single vocalisations were generated with the program SoundEdit (version 2.0.1, Farallon, see SCHMIDT et al., 1989) on a Macintosh IIci computer using a Sound Recorder device (Farallon). These sounds were sampled at 5 kHz with an FFT size of 1024 points.

2.2 Animals

The age classes proposed by GEISSMANN (1993) for captive gibbons and siamangs were used: infants from 0 to 2 years of age; juveniles 2.1 to 4 years; subadults 4.1 to 6 years; adults more than 6 years.

Song organisation of the following 5 pairs, groups or solitary animals were analysed in detail (group compositions and age classes given for the beginning of the study):

The adult pair *Na*+*Ga* at the Zürich Zoo consisted of the male ***Narong*** (*Na*), wild-born about in 1967, and the female ***Gaspa*** (*Ga*), wild-born about in 1963. The pair was together since July 1980.

The younger pair *Bh*+*Ch* at the Zürich Zoo consisted of the subadult male ***Bohorok*** (*Bh*) and his juvenile sister ***Chandra*** (*Ch*), both captive-born offspring of

Na+*Ra*, and both hand-reared at Zürich Zoo. *Bh* was born on 23 June 1975 and was 5 years and 5 months old at the beginning of this study. His sister *Ch* was born on 24 Dec. 1976 and was a 3 year 11 months old juvenile at the begin of this study. As her song repertoire and the temporal structure of her song vocalisations were not yet fully developed, the songs of this female were relevant to this study only because of her vocal and other interactions with the other study animals at Zürich.

Vreneli (*Vr*) was an adult female at Studen. She was wild-born about in 1963 and has remained solitary since both the offspring and her mate died in 1979.

The adult pair *Bb*+*Ra* at Studen consisted of the male ***Bobby*** (*Bb*), wild-born about in 1958, and the female ***Ratana*** (*Ra*), wild-born about in 1963. This pair was together since July 1980.

The family group *Ko*+*Cr*(+*Li*+*Al*) at the Studen Zoo consisted, at the beginning of this study, of the adult male ***Kobi*** (*Ko*), the adult female ***Christeli*** (*Cr*) (both wild-born about in 1963, and kept as a pair in Studen since about 1968), their juvenile daughter (*Li*), and their infant son (*Al*). *Cr* gave birth to a healthy male on 28 Dec. 1981.

2.3 Housing and Changes in Group Composition

At the beginning of this study, the two siamang groups at Zürich Zoo consisted of the pairs *Na*+*Ga* and *Bh*+*Ch*. On 14 July 1981 *Na* was transferred to Studen Zoo. In Zürich, his former partner *Ga* was paired with *Bh* on 12 Aug. 1981. Because *Bh*'s sister *Ch* was not considered yet to be sexually mature, she was kept with two hand-reared juvenile males (*Fa* and *Da*) after her separation from *Bh*, and with only one of them (*Da*) after 20 Nov. 1984.

In Zürich, the siamangs were kept in two adjacent indoor-cages (base area: 16 m^2 and 40 m^2; height: 4 m). In summer, both siamang groups were alternatively given access to a large outdoor cage (30 m^2 x 4.6 m). All cages were equipped with extensive bamboo scaffolding and ropes. Both groups could hear (but not see) each other at any time.

In Studen, the original constellation consisted of one solitary female (*Vr*), one pair (*Bb*+*Ra*) and one family group (*Ko*+*Cr*(+*Li*+*Al*)). On 14 July 1981, the adult male *Na* arrived from Zürich and was kept as a pair with *Vr*. On 8 Oct. 1981, *Bb* died of a Clebsiella infection.

During summer, all groups were kept in outdoor-cages (25 m^2 x 2.5 m) equipped with several horizontal stainless metal bars, ropes, and a wooden sleeping box. Two of the cages stood close together at a sharp angle. The third cage (of the family group) was located in a distance of more than 10 m. The sight from cage 3 to the other two cages was somewhat reduced by shrubs and trees. During winter, the siamangs were housed in a separate building. Two of the winter cages (18 m^2 x 2 m, and 14 m^2 x 2 m, respectively) were situated on the first floor and stood about 3.5 m apart; these two groups could see each other. The winter cage of the family group (6 m^2 x 3 m) was situated on the ground flour and could not be seen by the other two groups. As in Zürich, all groups could hear each other during the whole year.

2.4 Acoustic Terms and Definitions

A ***note*** is defined as "any single continuous sound of any distinct frequency (pitch) or frequency modulation, which may be produced by either an inhaled or exhaled breath" (HAIMOFF, 1984, p. 335). Based on the acoustic characteristics, these notes can be divided roughly into four groups or ***classes***: booms, barks, ululating screams and bitonal screams.

Note classes can be subdivided into different note ***types***. There are no strict borders between types of the same note class, and vocalising animals may gradually switch from one type to another. On the other hand, no intermediate forms were found between different note classes.

A ***phrase*** is a collection of several notes separated by short pauses of no more than 3 s duration and preferentially uttered in combination.

Larger song sections may differ from each other in the characteristic frequency of some phrases, note classes, or types, and in the variability of the rules governing note successions. These larger song sections are termed ***sequences*** (for an alternative definition of the same song sections see HAIMOFF, 1981, 1984).

A ***song*** is what fulfils the criteria set forth by THORPE (1961, p. 15): "What is usually understood by the term song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognisable sequence or pattern in time", or, a song is a succession of phrases with non-random succession probability ("Strophenfolgen mit nicht-zufälliger Folgewahrscheinlichkeit", TEMBROCK, 1977, p. 33). ***Song bouts*** are separated from each other by an arbitrarily defined interval of at least 5 minutes.

Some authors have referred to individual phrases within a song bout as "songs" (e.g. MARSHALL and SUGARDJITO, 1986). I recommend using the term "phrase" instead, in order to make it clear whether one is talking about a mere collection of notes (usually shorter than 1 minute), or about a song bout (i.e. a collection of phrases, with an overall duration of several minutes).

A ***duet*** occurs when one individual coordinates its vocalisations in time or type of vocalisation with those of another individual (SEIBT and WICKLER, 1982; WICKLER, 1974). Accordingly, a ***duet song*** is a song jointly uttered by two individuals and coordinated in time or phrases. A ***concert*** occurs when a song is uttered in coordination by more than two individuals, whereas a ***chorus*** is defined as a vocalisation bout without song structure, which is jointly uttered by more than two individuals (TEMBROCK, 1974, p. 189).

Various authors have created different terminologies for siamang song vocalisations. In order to facilitate comparison between the present study and earlier publications, the following description of vocalisations also includes cross-references to terminologies used by other authors.

3. Description of the Siamang Song Bouts

3.1 Description of Note Classes and Note Types

Unless noted otherwise, the classification of siamang song vocalisations used in this paper follows, and expands on, that of LAMPRECHT (1970) and HAIMOFF (1981). This classification is chiefly based on the physical characteristics and the temporal pattern, i.e. on structural and syntactical aspects (MARLER, 1965; TEMBROCK, 1974). The frequency and duration ranges of all types and classes of song vocalisations summarised in Table 2, and a sonagram of each is shown in Figure 1.

Table 2: Note classes and types used in siamang song bouts.

Class	**Type**	**Adult song repertoire** [1]	
		Male	**Female**
Booms	Grunts	+	+
	Short booms	+	+
	Long booms	+	+
	Ascending booms	+	(+)
Barks	Short fast barks	+	–
	Short slow barks	+	–
	Long barks	–	+
Ululating scream		+	(+)
Bitonal scream		+	–

[1] + = present, – = absent, (+) = produced by some females only.

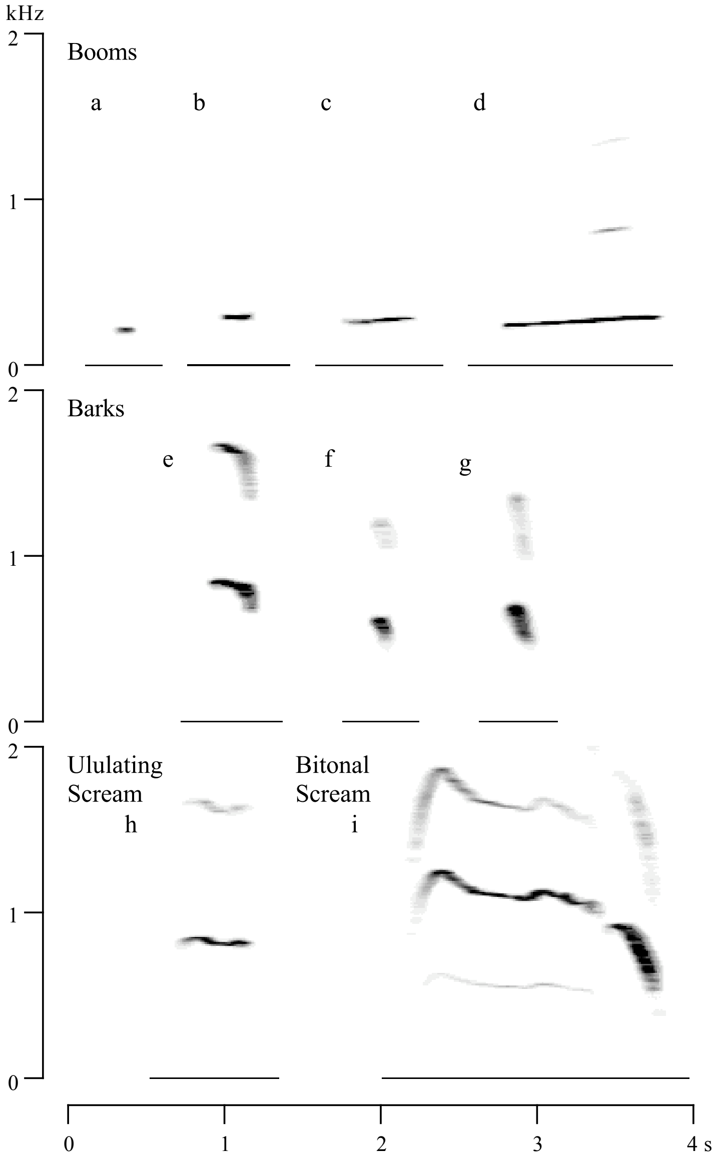

Fig. 1: Sonagrams of note classes typically produced during siamang song bouts, including booms (a = grunt; b = short boom; c = long boom; d = ascending boom), barks (e = long bark; f = short fast bark; g = short slow bark), ululating scream (h), and bitonal scream (i).

The frequency and duration ranges of all types and classes of song vocalisations are summarised in Table 3. For all siamang song vocalisations, the fundamental frequency is situated between 0.13 and 1.47 kHz. Only few such measurements have previously been published (HAIMOFF, 1983b, LAMPRECHT, 1970, SCHRÖPEL, cited in TEMBROCK, 1974, WEST, 1982). They largely support the data presented in Table 3. The frequencies published by BARKELL (1988), however, are all situated between 1 and 7.5 kHz. These values are not compatible with those presented here; apparently, BARKELL measured harmonics, not the fundamental frequency.

Table 3: Duration and frequency measures for note classes and note types used in siamang song bouts. [1] (Med = Median)

Class	N[2]	**Duration (s)**		**Fundamental frequency (kHz)**					
Type				**Minimum**		**Maximum**		**Modulation Range**	
		Med	**Range**	**Med**	**Range**	**Med**	**Range**	**Med**	**Range**
Booms									
Grunts	14	0.15	0.10-0.19	0.167	0.127-0.216	0.282	0.231-0.317	0.109	0.047-0.190
Short booms 1	11	0.09	0.05-0.11	0.301	0.259-0.346	0.371	0.361-0.410	0.074	0.060-0.110
Short booms 2	15	0.21	0.16-0.31	0.257	0.215-0.307	0.357	0.304-0.410	0.103	0.071-0.132
Short booms all	26	0.18	0.05-0.31	0.286	0.215-0.346	0.369	0.304-0.410	0.079	0.060-0.132
Long booms	12	0.50	0.28-0.69	0.225	0.203-0.270	0.314	0.279-0.491	0.084	0.053-0.222
Ascending booms	14	0.55	0.46-0.89	0.224	0.194-0.239	0.335	0.276-0.377	0.111	0.064-0.153
Barks									
Short fast barks (SFB)	14	0.14	0.11-0.15	0.375	0.333-0.463	0.808	0.742-0.869	0.405	0.361-0.488
Short slow barks (SSB)	19	0.13	0.10-0.16	0.385	0.311-0.438	0.720	0.670-0.831	0.346	0.289-0.467
Long barks (LB)	12	0.25	0.17-0.33	0.573	0.493-1.135	0.798	0.691-1.472	0.214	0.120-0.371
Ululating scream (US)									
US I	12	0.61	0.38-0.72	0.648	0.508-0.808	0.913	0.773-0.978	0.221	0.113-0.470
US II	14	0.74	0.32-1.25	0.642	0.340-0.816	0.878	0.807-0.956	0.226	0.093-0.500
Bitonal scream (BS)									
BS, first phase	13	1.05	0.67-1.40	0.463	0.357-0.486	0.598	0.486-0.824	0.128	0.076-0.349
BS, second phase	13	0.48	0.30-0.68	0.477	0.415-0.780	0.892	0.766-1.008	0.377	0.120-0.510

[1] Short booms 1 are booms occurring during the "locomotion call" of the great call sequence; short booms 2 are those immediately preceding ululating screams. The long booms measured here are those occurring at the beginning of the female's great call phrase, while the ascending booms were those at the beginning of the ululating scream II phrase. Long barks were measured at the beginning of the female great call, and short barks at the end of the ululating scream II phrase.

[2] N = number of calls = number of individuals (i.e. one call was analysed per individual), except for "grunts": 14 grunts of 11 individuals, and "short booms all": 26 calls of 15 individuals.

3.1.1 Booms

Equivalent terms: "Heullaute" (LAMPRECHT, 1970); "howling" (SCHRÖPEL, cited in TEMBROCK, 1974); "booms" (CHIVERS, 1974; FOX, 1977; HAIMOFF, 1981).

Booms are "ooo"-like notes of low frequency. They are usually produced with the mouth closed (or nearly closed) and maximally inflated throat sac or during inflation of the throat sac. Longer booms (see below) are mostly produced while the vocalising animal is stationary (in sitting or hanging position). On the basis of their duration, frequency modulation and association with other vocalisations, a number of different types of booms can be differentiated. Because all possible transitional forms occur, booms cannot always be attributed to a single type. This finding contrasts with the view offered by HAIMOFF (1983a, p. 68), who defined the various types of booms as completely segregated vocalisations without overlap. The following four types of booms are recognised here: grunts, short booms, long booms, and ascending booms, which may occur in different contexts.

a) Grunts (Fig. 1a):

Grunts (HAIMOFF, 1983a, p. 73; "glunks", FOX, 1977, p. 453) are short, soft vocalisations. Although BRICKNELL (1992) and CHIVERS (1974, p. 237) described them for females only, grunts are uttered by siamangs of either sex. The throat sac is only minimally inflated during grunts. In the sonagrams, grunts resemble short booms, but their intensity is much lower. Grunts are produced at the beginning of a song bout. Grunts are also uttered while feeding (CHIVERS, 1976, p. 119; FOX, 1977, p. 442), when the siamang see the keeper arriving with food, or in early stages of an alarm reaction ("soft grunts", CHIVERS, 1976, p. 119).

b) Short booms (Fig. 1b):

Short booms usually occur as single notes, in series, as the second note in a pair of booms (corresponding to "diphasic"-booms in CHIVERS, 1974), or immediately prior to a bark, an ululating scream, or a bitonal scream. Short booms differ in their duration and frequency characteristics depending on context and several distinct types of short booms could possibly be recognised. For instance, short booms occurring during very rapid barking (SFB) are much shorter and show less frequency modulation than booms occurring immediately prior to a ululating scrteam II (see "short booms 1" and "short booms 2", respectively, in Table 3).

c) Long booms (Fig. 1c):

These booms occur as single notes, as the first note in a pair of booms, and prior to long barks. Some females, however, produce only short booms in the latter context.

d) Ascending booms (Fig. 1d):

Ascending booms (HAIMOFF, 1981, 1983a) are long booms of an increasing frequency modulation. They occur almost exclusively in the first position within pairs of booms. These pairs occur in three different contexts: 1. as single elements within the song, 2. immediately prior to an ululating scream, or 3. during the initial phase of a great call sequence prior to the bitonal scream (see below). Whereas short and long booms are produced by male and female siamangs, HAIMOFF (1981) described ascending booms only for males. As a rule, this type of vocalisation is, in fact, produced by males only, but some of the females studied here frequently produced ascending booms (e.g. one female each in Doué-La-Fontaine, Studen, Taman Safari/Cisarua and Twycross).

The use of bi-phasic notes (alternate production of exhalation and inhalation sounds) during the song probably represents a primitive characteristic for both male and female gibbon vocalisations (GEISSMANN, 2000). Previous authors disagreed on whether all notes in the song of adult siamangs are produced during exhalation (Haimoff, 1981; LAMPRECHT, 1970) or whether some of them (the boom notes) are produced during inhalation (TEMBROCK, 1974, p. 178; WELCH, 1911, p. 358). During the boom notes, the throat sac is inflated; this could be occurring through either exhalation or inhalation. Close observation of several siamang pairs during the present study indicates, however, that at least some booms may be produced during inhalation. The visible contractions of ventral rump muscles of vocalising siamangs suggest that the alternation of barks and booms during the acceleration of the female great call phrase consist of an alternation of exhalation (barks) and inhalation (booms).

This interpretation is further supported by observation of an adult female hybrid between a Mueller's gibbon and a siamang (*H. muelleri* x *H. syndactylus*). Like most gibbon species, this female hybrid had no visible throat sac. During the acceleration of its great call, the female produced bi-phasic notes clearly consisting of sounds alternatingly produced during exhalation (low frequency) and inhalation (high frequency). This finding is relevant, because species-specific characteristics of gibbon songs are largely inherited (BROCKELMAN & SCHILLING, 1984; GEISSMANN, 1984, 1993). As Mueller's gibbons do not produce inhalation notes during their great calls (Geissmann, 1993), the occurrence of this characteristic in the hybrid suggests that it was inherited from the siamang parent and provides indirect support to the hypothesis that inhalation notes typically occur in the siamang great call. It remains unknown, however, whether booms other than those emitted during the great call acceleration are inhalation notes.

3.1.2 Barks

Equivalent terms: "Bellaute" (LAMPRECHT, 1970); "barking sounds" (SCHRÖPEL, cited in TEMBROCK, 1974); "barks" (CHIVERS, 1974; FOX, 1977; HAIMOFF, 1981).

Together with booms, barks comprise the most frequent vocalisations in the siamang song. Barks are produced as single notes or in series but almost every bark is preceded by a short boom. During barks, the mouth is opened moderately and the teeth remain hidden behind the lips. As in booms, the various types of barks are parts of a graded system and are linked by barks of intermediate characteristics.

a) Long barks (Fig. 1e):

In adult siamangs, this type of vocalisation is produced by females only (although this has been questioned by FOX, 1977) and is, as a rule, uttered in accelerated series. The acceleration is created by a gradual reduction in the duration of the barks as well as of the intervals between the barks. With increasing speed and intensity, the long barks continuously change into short, fast barks (see below, type b). In parallel with the acceleration, the booms which precede each bark become shorter and rise in frequency. This rise ("raised bass", MARSHALL and MARSHALL, 1976) is not equally pronounced in all females; in some animals it can hardly be heard. Long barks are called "high barks" by MAPLES et al. (1989). During this vocalisation, females usually remain stationary or move around only slowly.

b) Short fast barks (Fig. 1f):

In contrast to long barks, these other types of barks are produced by animals of either sex. Short fast barks often develop out of long barks during the acceleration described above. Independent series of short fast barks also occur frequently during the song. During these very fast strings of vocalisations, the mouth of the calling animal is not completely closed between the single barks. During series of short fast barks, siamangs frequently exhibit rapid, vigorous locomotion, hence the name "locomotion call" proposed by HAIMOFF (1981). In contrast to this observation, BENCHLEY (1942, pp. 24, 27) reports that siamangs sit still during their songs.

c) Short slow barks (Fig. 1g):

Like the previous type of barks, short slow barks are produced by animals of either sex. This bark can be uttered as a single sound or in series, often with irregular intervals. When producing short slow barks, siamangs usually remain stationary or move around slowly. This type of vocalisation may continuously develop out of short fast barks (type b) or, less frequently, out of long barks (type a). Short slow barks are probably identical to the "barking sound of medium length" described by SCHRÖPEL (cited in TEMBROCK, 1974, p. 187).

3.1.3 Ululating scream

Equivalent terms: "Jauchzer" (LAMPRECHT, 1970); "rejoicing" (SCHRÖPEL, cited in TEMBROCK, 1974); "cry" (FOX, 1977); "ululating scream" (HAIMOFF, 1981); "undulating scream" (WEST, 1982).

This long note of slightly decreasing frequency (Fig. 1h) is produced with a fully inflated throat sac and a widely opened mouth. The teeth are not bared, however. This sound is never uttered in series. The vocalising animal is stationary or moving around slowly.

The ululating scream is nearly always produced in association with other types of vocalisation, thus producing a short combination of notes corresponding to the term "phrase" in HAIMOFF (1984) or the term "Motiv" in THIELCKE (1961). Ululating screams of all animals of this study are preceded by a pair of booms, the first of which is an ascending boom, the second a short boom. The second boom precedes the scream so closely that no interval is perceived by the observer, similar to the situation in many booms preceding barks. Following the ululating scream, the siamang almost invariably utters a brief series of short fast barks.

Individual characteristics are particularly striking in the ululating scream phrase and become manifest in the duration of the interval between the ascending and the short boom (or between the ascending boom and the ululating scream, respectively), in the number of short barks following the ululating scream, and in the frequency modulation of the ululating scream itself. Whereas these parameters clearly varied individually, they remained relatively constant in the song bouts of each animal. For example, one of the adult males of this study never produced the series of short barks after his ululating screams. Similar individual characteristics were also mentioned by LAMPRECHT (1970, p. 197) for some of his study animals.

Two variants of ululating screams are recognised in this study: (1) ululating screams occurring in the middle of the great call sequence (US-I), and (2) ululating screams occurring at the beginning, at the end or outside of the great call sequence (US-II).

The two variants are more or less distinct – depending on the animal – in the duration and the frequency modulation of the scream note, but also in the number of short barks following the scream. In some males, no clear difference in the acoustical structure of the two screams was obvious.

Many individuals terminate the US-II phrase by an additional pair of booms. Like the pair of booms which introduces the phrase, this final pair of booms consisted of an ascending boom followed by a short one in the study animals; only the adult male *Na* frequently omitted the short boom. In the adult male of HAIMOFF's (1981) study, the ascending boom was followed by a long boom instead of a short one.

In the studies of FOX (1977), HAIMOFF (1981) and LAMPRECHT (1970), only males were observed to produce ululating screams. In the majority of the animals studied I observed, this rule appeared to hold true. Several females, however, regularly produced ululating screams in their songs, always of the variant II (e.g. one female each in Doué-La-Fontaine, Studen, Taman Safari/Cisarua, Twycross and Zürich). These screams did not fall outside the range of variability of male ululating screams and also included the whole ululating scream phrase described above. The female observed by SCHRÖPEL (cited in TEMBROCK, 1974) also appears to have used this class of vocalisation frequently.

The vocalisation termed "'ululating' call" in BARKELL (1988, p. 3) is completely different from the one described above. BARKELL's description of the sound and the degree of the vocalising animal's mouth aperture perfectly fit, in fact, another class of vocalisation which is discussed below: the bitonal scream.

3.1.4 Bitonal scream

Equivalent terms: "Schrei mit anschliessendem Jauchzer" (LAMPRECHT, 1970); "climax" (FOX, 1977); "bitonal scream" (HAIMOFF, 1981).

This vocalisation consists of two different phases (hence the name "bitonal") which differ in their frequency and which follow each other with only a minimal time interval. By the definition used in this paper, they are two different notes. Because both are consistently linked with each other and because of the transition mechanism discussed below, it appears logical to combine them both under the same class of vocalisations.

The first phase of the bitonal scream consists of a drawn out note of a duration of 0.67-1.40 s, and of relatively constant frequency. During this sound, the throat sac is maximally inflated, and the mouth is opened widely, with bared teeth. The second phase is quite variable in frequency modulation. As a rule, it is considerably shorter (0.30-0.68 s) than the first phase, and usually of decreasing frequency. The throat sac is not in maximal inflation, the teeth are not bared. Bitonal screams are never uttered in series.

LAMPRECHT (1970, p. 188) was the only author to treat the two phases as two distinct vocalisations. He called the first phase "Schrei" and considered the second phase as being identical to the ululating scream. In most siamangs, however, the second phase of the bitonal scream differs in its frequency structure from the ululating scream and is usually shorter than the latter (see Table 3 and Figure 1).

To human observers, the first phase of the bitonal scream always appears to be of lower frequency than the second. Interestingly, both LAMPRECHT (1970) and HAIMOFF (1981, 1983b) observed just the opposite on their sonagrams: The fundamental frequency of the first phase appeared to be higher (0.96-1.25 kHz) than that of the second phase (0.42-1.00 kHz). HAIMOFF (1981, 1983b, 1984) suggested that the real fundamental frequency of the first phase is filtered away or suppressed by antiresonance and, hence, only the second harmonic was visible on sonagrams. This effect is, apparently, neutralised when the throat sac is deflated during the second phase of the bitonal scream.

During this study, however, high quality tape-recordings of songs of various siamang males (e.g. *Na* and *Bh*) made it possible to see a very weak additional frequency band below what has previously been believed to be the fundamental frequency of the first phase of the bitonal scream (the lowest of the 3 bands visible in Fig. 1i). This weak band appears to be the real fundamental frequency of this phase. Its intensity is considerably lower than that of the first harmonic, suggesting that the fundamental frequency is at least partially filtered away. The high frequency attributed by LAMPRECHT (1970, p. 188) and WEST (1982, p. 16) to the first phase of the bitonal scream (1.13-1.21 kHz and 1.08-1.23 kHz, respectively), refers, therefore, to the first harmonics (as correctly suggested by LAMPRECHT, 1970), and not to the fundamental frequency. According to the measurements carried out in the present study, the real fundamental frequency of the first phase of the bitonal scream is situated between 0.36 and 0.82 kHz and is clearly lower than that of the second phase (0.42-1.00 kHz).

The captive male siamang observed by BRICKNELL (1992) produced bitonal screams, in which no first phase was visible on the sonagrams at all, and with the second phase "starting at a frequency of 1.8 kHz and ending at 1.3 kHz". This range is situated above that of all males heard during the present study (0.42-1.00 kHz). The bitonal screams uttered by that male appear to be atypical.

The bitonal scream is almost always combined with locomotion. Usually, the calling animal moves only a short distance, by swinging itself to another branch or sitting place; sometimes the animal merely changes its position.

Similar to the ululating scream, the bitonal scream is associated with other vocalisations, thus forming a particular phrase. The phrase begins with a short boom, or – in some individuals of this study – a pair of booms consisting of an ascending boom followed by a short boom. After the short boom, the animal utters its bitonal scream, which is in some animals followed by a number of short fast barks. The bitonal scream phrase is, therefore, similar to the ululating scream phrase in its structure. Here, too, some individual characteristics are evident. They include the frequency modulation, the intensity of the scream, and the number, structure and interval duration of its accompanying phrase elements. In this study, the two males *Bh* and *Na* produced a short series of 1-4 short fast barks immediately after the scream, whereas no barks were uttered after the bitonal screams of another male (*Bb*). These particular barks also appeared to be missing in the males observed by HAIMOFF (1981), MAPLES et al. (1989) and WEST (1980), as well as in two of four males in LAMPRECHT's (1970, p. 197) study. One of the males of this study (*Bb*) always produced the first phase of his bitonal scream so softly, that it was sometimes difficult to hear when the male was duetting with a female. The second phase of this male's bitonal scream, however, was of the normal intensity. In exceptional cases, all males can omit the second phase of the bitonal scream. One of the males observed by WEST (1980, p. 12) in Sumatra always produced only the first phase.

It is not clear, whether the two phases of the great call are both produced during exhalation, as suggested by Haimoff (1981, 1983b), or whether one phase is an inhalation note.

The bitonal scream is only known from male siamangs. RÜHMEKORF (1963) described bitonal screams of a female siamang, but, at that time, the sex of this animal could not be determined with certainty, but later, the animal was identified as a male (RÜHMEKORF, pers. comm.).

3.2 Song Bout Organisation

The composition of a typical siamang song bout is organised according to relatively strict rules. At the highest level of subdivision, the song bout consists of 4 different types of sequences which occur in a predetermined order, as shown in Figure 2. After the grunting sequence and the introductory sequence, the song bout consists of two sequences which are repeated in alternation until the end of the song bout: the interlude sequence and the great call sequence. Additional information on the organisation of the sequences can be found in BRICKNELL (1992), HAIMOFF (1981), LAMPRECHT (1970) and ORGELDINGER (1999).

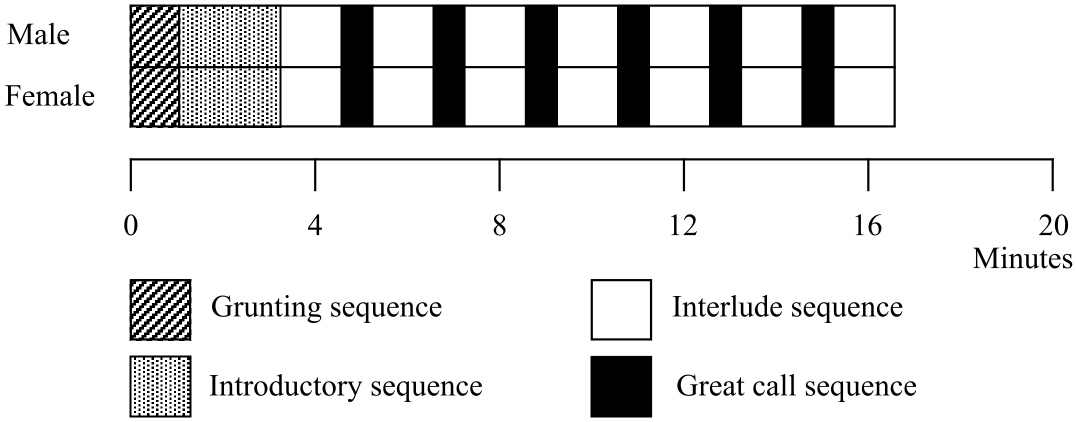

Fig. 2: Stylised diagram illustrating the sequential nature of the duet song bout produced by adult siamang pairs (after HAIMOFF, 1984, supplemented).

3.2.1 Grunting sequence

At the beginning of a song bout, siamangs usually utter only soft grunts for a few minutes (Figures 2 and 3). These vocalisations have been mentioned in earlier studies (BRICKNELL, 1992; CHIVERS, 1974, p. 237; FOX, 1977, p. 453; HAIMOFF, 1983a, p. 73; WEST, 1982, p. 6), but were not regarded as being part of the song bout, and the organisation of these series of grunts has apparently not been analysed.

Because the grunts typically occur at the beginning of the siamang song bout and because they essentially appear to be soft booms (which are typical song elements), this study regards the grunts as part of the song. It is unknown, however, whether mates coordinate their grunts (i.e. whether they are duetting during this sequence). The grunting sequence may have been neglected in earlier studies of siamang singing behaviour, because a similar sequence does not appear to exist in the duet songs of other gibbon species.

Although some authors heard grunts only being uttered by females (BRICKNELL, 1992; CHIVERS, 1974), the males of the present study also participated in the grunting sequences. It should be mentioned that the grunting sequence may sometimes be missing and the siamangs may directly start their song with the barks and booms of the introductory sequence (see below). In other instances, one animal was observed to grunt alone for some time before it was joined by its partner. Grunts may also occur in other contexts (section 3.1.1). In general, grunts appear to indicate that the calling animal is moderately excited.

3.2.2 Introductory sequence

The beginning of the proper song bout (i.e. after the grunting sequence) consists, according to the traditional view, of the “introductory sequence“ (HAIMOFF, 1981). Like the grunting sequence, the introductory sequence is produced only once at the beginning of a song bout. It consists mainly of short single barks, short series of barks, and short booms (and occasionally other types of booms). During the sequence, mated siamangs appear to synchronise their barks or bursts of barks (Figure 3).

3.2.3 Interlude sequence

Equivalent terms in previous publications: "Zwischenphase" (LAMPRECHT, 1970); "organizing sequence" (HAIMOFF, 1981); "interlude sequence" (HAIMOFF, 1988).

The interlude sequence has a typical duration of 5-60 s; in exceptional cases it can be extended to up to several minutes. The organisation of this sequence is very variable (Figures 3 and 5) and is combined of booms (types a-c), barks (types b and c) and ululating screams (US-II). In this study, the term "interlude sequence" refers to a shorter song segment as compared to the definition used in HAIMOFF (1981) and LAMPRECHT (1970): After each great call, males (and sometimes females, too) utter a US-II phrase. Because the interval between the phrase and the great call has an individually constant duration, the US-II phrase is considered here to be part of the great call sequence; whereas HAIMOFF (1981) and LAMPRECHT (1970) treated it as part of the interlude sequence.

The organisation of the interlude sequence can show considerable differences between song bouts of the same pair. The interlude sequences may include many elements of a particular type of vocalisation in one song bout, but only a few in another song bout. Many different note combinations have been observed to occur during interlude sequences. HAIMOFF (1981, p. 136) suggested that these combinations occurred at random, but this has not yet been analysed.

Siamangs frequently exhibit locomotion during the interlude sequence. Phases of rapid locomotion occured especially during the short fast barks (type b). These series of barks were often produced in synchrony by mated pairs, but sometimes females accompany the males' short fast barks with short slow barks only. Every bark note is usually introduced by a short boom. In addition, pairs of booms are frequently produced during the interlude sequence. As a rule, the first boom of the pair is an ascending one (if produced by a male), or a long boom (if from a female), and the second boom is a short one. The ululating screams are usually uttered in combination with other notes so as to form a US-II phrase (as described above).

3.2.4 Great call sequence

Equivalent terms in previous publications: "Duett" (LAMPRECHT, 1970; "great call sequence" (HAIMOFF, 1981).

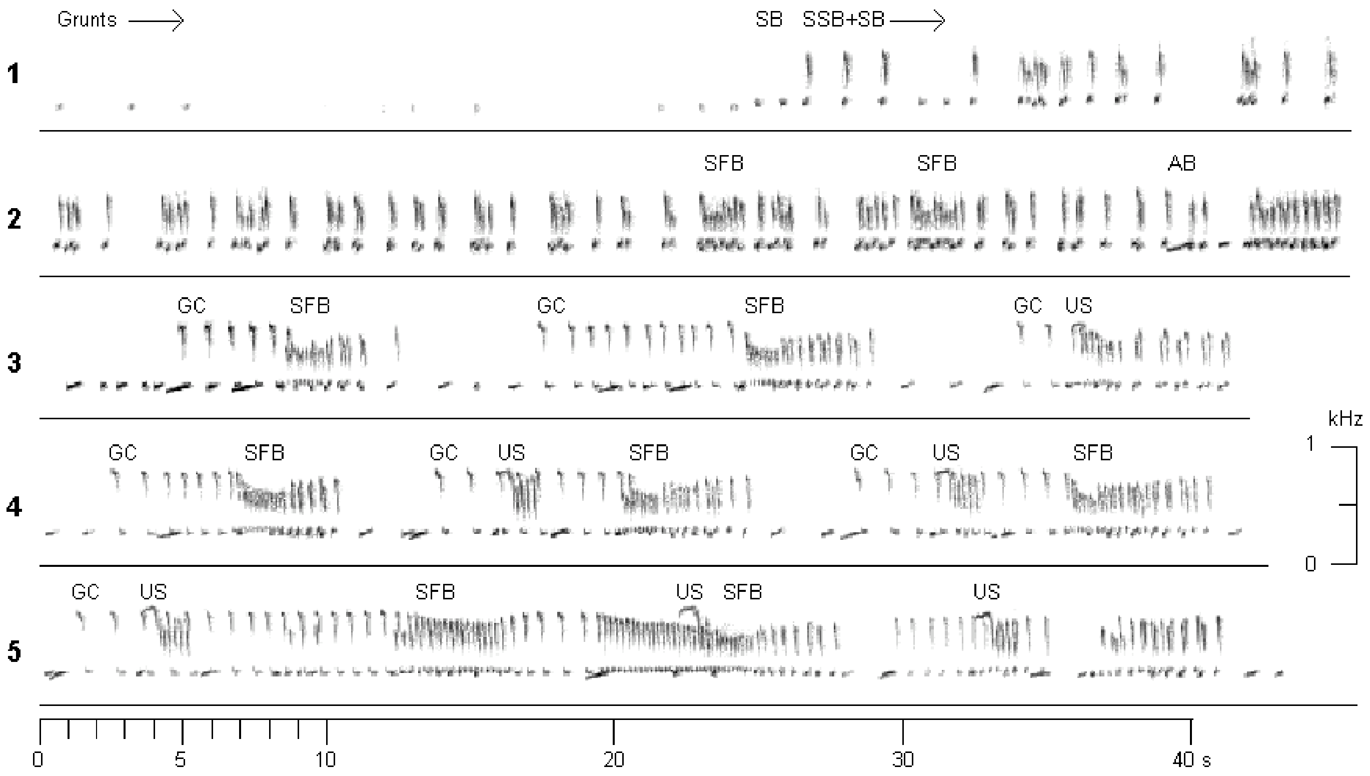

Fig. 3: The early stages of a duet song bout of pair *Bh+Ga*. The sonagrams represent a continuous sequence, beginning with the grunting sequence (line 1). At the end of the sequence (at about 25 s on line 1), the grunts change into booms (SB). The first barks (SSB) mark the end of grunting sequnce and the beginning of the introductory sequence (at about 26.5 s on line 1). The first occurrence of an ascending boom (AB) indicates the end of the introductory sequence and the beginning of the first interlude sequence (at about 39 s on line 2). The first great call sequence begins on line 3 (GC). Lines 3-5 show the first 7 great call sequences of the song bout, each followed by an interlude sequnce. The female aborts each great call before completion except the last one, and all great call sequences lack the full set of male contributions which is found in typical great call sequences later in the song bout, i.e. after the first bitonal scream of the male (see Fig. 5). Abbreviations: AB = ascending boom (only the first one of this song bout is labelled in the sonagram); GC = start of a female great call; SB = short booms; SFB = short fast barks; SSB = short slow barks; US = ululating scream of the male.

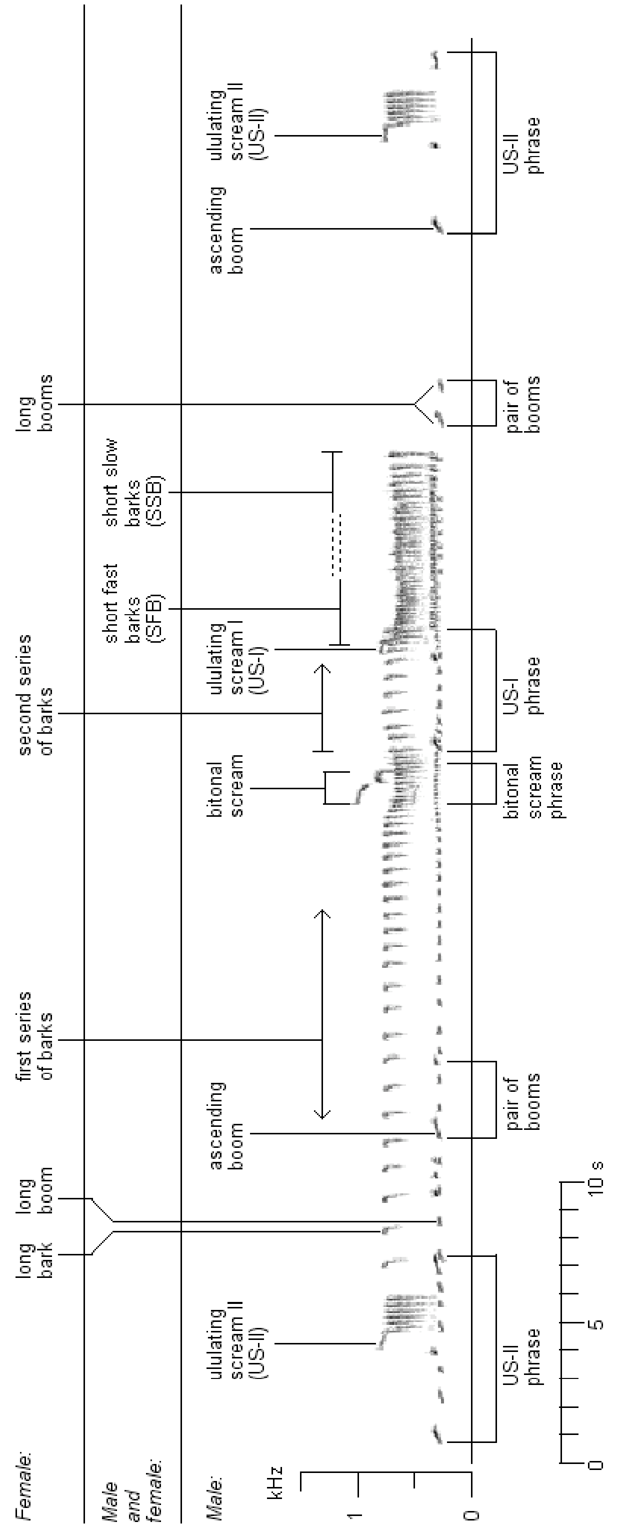

Fig. 4: Organisation of a typical great call sequence of pair *Na+Ga*. Selected notes or groups of notes are individually indicated.

The great call sequence has a duration of about 20-50 s. It includes the great call, which consists of two series of accelerated barks produced by the female. At certain points in each series of barks, the male inserts particular combinations of vocalisations (LAMPRECHT, 1970). The organisation of a typical great call sequence is shown in Figure 4. The term "great call" was originally coined by BOUTAN (1913, p. 33: "grand chant d'excitation") for a particular series of vocalisations produced by a female white-cheeked gibbon (*H. leucogenys leucogenys*).

Great calls are associated with of female siamangs only, at least as far as adult animals are concerned. BARKELL (1988, p. 3) reports great calls of male siamangs, but her (unfortunately very indistinct) sonagram of that phrase (her Figure 3) rather resembles the final half of an ululating scream phrase, whereas her description of the "'ululating' call" clearly can be identified as a bitonal scream.

The great call sequence is a combination of vocalisations of all classes. Some vocalisations are produced exclusively during this sequence, such as the long barks (type a), the ululating scream variant I, and the bitonal scream.

A series of booms ends most interlude sequences and marks the beginning of the next great call sequence. The males of this study usually produced pairs of booms during this part of the song bout. These booms resembled those produced during the

US-II phrase: an ascending boom followed by a short boom. Indeed, the booms at the transition from the interlude to the great call sequence are frequently part of a US-II phrase. In many cases, the male's short boom is immediately followed by an ululating scream, while the female has already started the long barks which are part of the great call. The ululating scream leading from the interlude sequence to the great call sequence can be seen in Figures 4 and 5, but also on the sonagrams in LAMPRECHT (1970, p. 191) and MARSHALL and MARSHALL (1976, p. 236). The male studied by HAIMOFF (1981, p. 136f) produced pairs of booms in this part of the song bout, but these pairs of booms consisted of an ascending boom followed by a long boom, instead of a short one.

The pairs of booms, as well as the ululating scream which often follows them, show a very constant temporal relationship to the female's great call. A constant timing is typical of song elements produced during great call sequences. Although either the booms and the "initial" US-II phrase are not always produced at the beginning of the great call, they are attributed to the great call sequence in this study.

At the beginning of a great call sequence, the duetting siamangs are stationary (i.e. either sitting or hanging by their hands). The female begins the great call with a rhythmic series of long barks. Each of her barks is introduced by a boom (usually long booms). This first series of barks is continuously accelerated by shortening the duration of the barks and the intervals between them. In synchrony with the female's barks, the accompanying booms are shortened. During the long barks, the male typically produces only the ascending boom which announces his bitonal scream. This boom, however, may be absent, as is usually the case in the songs of the male *Na*. During the acceleration, the long barks continuously change to short fast barks. Near the end of the first series of barks – at the climax of the acceleration – the male inserts his bitonal scream.

The bitonal scream is usually produced during locomotion: In most cases, the male swings to another place in the cage. The female, too, becomes more active and begins to brachiate around with increasing speed of her barks. Occasionally, both animals may confine themselves to a change of their positions. The order of these events is variable: in most cases, it is the male who starts locomoting; this is followed by his bitonal scream, and finally, the female begins to brachiate. A frame-by-frame analysis of the film recordings demonstrated, however, that sometimes the female starts to locomote before the male, unlike the siamang pair observed by HAIMOFF (1981, p. 139).

After his bitonal scream, the male often utters a few short barks and then immediately begins with the US-I phrase: It produces the pair of booms (ascending boom, then short boom) which introduces the ululating scream.

With the end of the male's bitonal scream, the female begins a second accelerated series of barks, by which time both animals have returned to a stationary position. Again, the second series of barks begins with long barks, which gradually change to short fast barks during the acceleration. This series of barks, however, begins with a faster rhythm, and the acceleration sets in earlier than in the first series. At the climax of the second series, the male sets in with his ululating scream. He finishes the US-I phrase and then immediately joins the female in her short fast barks. In this phase of the great call sequence, both animals exhibit the fast, vigorous brachiation display ("Umhertoben", LAMPRECHT, 1970, p.193) which is typical for the "locomotion call". In a pair observed by MAPLES et al. (1989), the female hardly participated in this locomotion display.

After a few seconds, the pair's series of short fast barks is replaced by short slow barks, and finally, the barking stops completely. Both animals then produce a few booms. Those of the female usually include, among others, a long boom; those of the male include a pair of booms which represents the introduction of the US-II phrase which concludes the great call sequence.

Some females tend to accompany the ululating scream of their mate with a few short slow barks, the occurrence of these notes as well as the duration of the interval since the preceding vocalisations are very variable. The end of the great call sequence is, therefore, arbitrarily defined to be situated at the end of the male's US-II phrase. The concluding US-II phrases of the male were lacking in 19 out of 20 great call sequences of the pair "*Ulli*" and "*Tilly*" at Frankfurt Zoo (tape-recorded on 19 and 20 Sept. 1981). In this respect, the great call sequence of the Frankfurt male appears to differ from that of other siamangs. The US-II phrase is produced by all other males whose songs I was able to analyse, as well as by some of the females (e.g. *Vr*).

The great call sequence is a complex, ordered chain of interactions between the mates: At certain predictable points in the sequence, each animal utters certain types of vocalisations in a particular temporal pattern, and exhibits particular types of locomotion. The order of these interactions follow the same pattern in all pairs of this study.

Some adult siamangs were observed to hold a hand or an arm in front of their mouth (or in front of the throat sac) during certain of their song vocalisations. The male "*Ulli*" (Frankfurt Zoo) did this during many of his bitonal screams, US-I and -II phrases and series of short fast barks. The females "*Tilly*" (Frankfurt), *Ga* (Zürich) and *Ra* (Studen), typically exhibited this behaviour during their great calls (i.e. during both series of long barks). This particular behaviour has also been described by BADRAUN et al. (1998), BRICKNELL (1992), FOX (1977), HESS-HAESER (1971), LAMPRECHT (1970), RÜHMEKORF (1963) and SCHIRMEIER (1966). Its functional significance is unclear.

The male's main vocal contributions during the female's great call consist of the bitonal scream phrase, followed by the US-I phrase (see Figure 4). This is the characteristic order of vocal events which has been described first by LAMPRECHT (1970). It has later been confirmed by HAIMOFF (1981), MAPLES et al. (1982) and WEST, 1982, p. 13ff) and also corresponds to the typical sequence I heard in 17 additional siamang pairs in various zoos. Only FOX (1977) reported that the siamang males in her study produced their screams in the opposite order of the one described by LAMPRECHT (1970). Her description of the great call sequence makes it obvious that she had applied LAMPRECHT's term "Schrei" (i.e. the bitonal scream) to the "Jauchzer" (i.e. the ululating scream), and *vice versa*; It can, therefore, be concluded that both authors had observed the same order of male vocalisations during the great call sequence.

The great call sequence is variable; numerous variations of the typical pattern are possible. These variations occur mainly at the beginning of a song bout, and the first great call sequences are frequently aborted (HAIMOFF, 1981, 1988).

The first attempts of great call sequences during a song bout usually consist of a few long barks of the female. The number of barks progressively increases during subsequent great call sequences. The early series of long barks are not accelerated and are frequently not accompanied by the typical male vocalisations. During the early series of long barks, the male may not vocalise at all, or confine his contribution to short fast barks. In subsequent great call sequences, US-II contributions occur with increasing frequency. In later great call sequences, the male produces his introductory vocalisations, the long barks of the female are produced in accelerated series, and several series are occasionally sung in succession. Finally, the typical male contributions occur during the climaxes (i.e. bitonal scream and US-I phrase).

As shown above, the great call sequence develops at the beginning of the song bout from single long barks to the full complex sequence by a progressive addition and elaboration of components. This development does not necessarily show a linear course. Occasionally, the animals may fall back from a relatively complex stage of sequence development to a simpler form and recapitulate the development. Similar fluctuations have been described for the development of the frequency-modulated male phrases of the yellow-cheeked gibbon (*H. gabriellae*) (GOUSTARD and DEMARS, 1973, p. 181).

Once the great call sequence is fully developed, it remains essentially constant until the end of the song bout (Figure 5), although untypical or aborted sequences may occasionally occur.

Individual-specific characteristics in the structure of single vocalisations have been mentioned above. In addition to these, some individuals may also be recognised by the note combination used during the great call sequence. Males may differ in the number of short barks produced during an ululating scream phrase, females may differ in the duration of their series of long barks, the speed of barking at the beginning of these series, or the extent of their acceleration etc. (for additional examples see CHIVERS, 1974, p. 238ff; FOX, 1977, p. 458f; LAMPRECHT, 1970, p. 197; WEST, 1982, p. 13ff).

The various vocalisations of the great call sequence are not only uttered in a constant order, but also with constant intervals between the notes. These intervals show individual-specific durations. For instance, the means intervals between the initial long barks of great calls produced by *Vr* (0.76 s) were about twice as long as those produced by *Ra* (0.34 s; $p < 0.001$; Mann-Whitney U Test). In the US-I phrase of *Na*, the interval between the ascending boom and the ululating scream had a mean duration of 3.2 s, in *Bh* it was 2.6 s ($p < 0.01$; Mann-Whitney U Test). Additional examples of individual-specific intervals can be found in GEISSMANN (1999), LAMPRECHT (1970, p. 195) and WEST (1982, p. 22).

Vocalisations of duetting animals are coordinated in time and type of vocalisation. Mated siamangs not only synchronise the beginning and end of their song sequences, but also exhibit a complex structure of vocal interactions within the sequences. This coordination includes the types of vocalisations used by both animals, as well as time intervals in the vocal interactions. In order to support the constant relationship between their vocalisations, both mates must synchronise their vocalisations from time to time. LAMPRECHT (1970) discovered at least four points where this happens within the great call sequence. HAIMOFF (1981) suggested that the male's pairs of booms at the beginning of the great call sequence initiate the beginning of the female's great call, and that similar pairs of booms uttered during the female's first series of long barks may initiate the acceleration of these barks. Pair-specific characteristics also exist in the vocal interactions of mated siamangs (LAMPRECHT, 1970). At least some of these pair-specific characteristics are not just identical with individual-specific song characteristics, but are created by each siamang adapting its song to that of its partner (GEISSMANN, 1999).

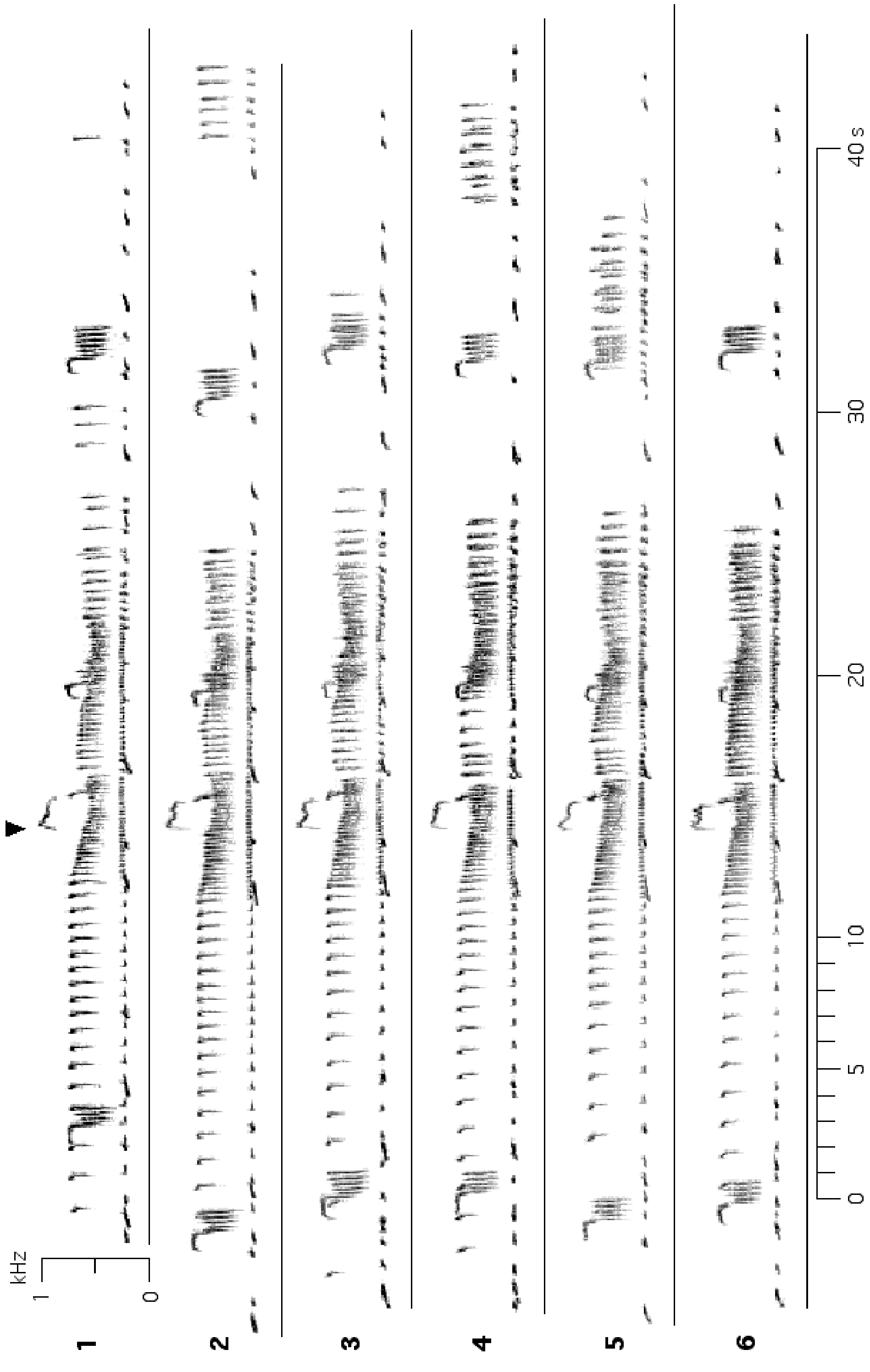

Fig. 5: The first 6 great call sequences after having reached their stable form (after the first bitonal scream of the male) and the 6 subsequent interlude sequences of a song bout of pair *Bh+Ga*. The sonagrams represent a continuous sequence immeadiately following the one shown in Figure 3. Each line begins with a great call sequence and ends with an interlude sequence. Sonagrams are aligned by the bitonal screams (arrow) of the male *Bh*.

3.2.5 "Corrections"

Incomplete or atypical great call sequences occurred in all siamang pairs of this study. If one partner produced an atypical contribution to a great call sequence, the sequence was often either aborted, or continued in a way that the atypical contribution was corrected or compensated for. An example of this is presented here: If the male inserted his bitonal scream *before* the acceleration of the female's first series of barks, he would sometimes abort his premature contribution in mid-scream, wait for the acceleration of his partner's barks, and then insert a second scream in the proper place. As an alternative way of correcting the male's premature insertion of a bitonal scream, the female sometimes quickly caught up by immediately producing her acceleration in a foreshortened fashion, beginning a second series of barks and accelerating it so soon that the male could insert the ululating scream-I in the typical interval after his bitonal scream. Similar observations on siamang song variation and correction have been reported by HAIMOFF (1981, 1988) and MAPLES et al. (1989) and are also known of other gibbon species (HAIMOFF, 1984, 1988).

3.3 Alarm Call Bouts

Although superficially similar to song bouts, alarm call bouts are not songs according to the definition followed in this paper (see section 2.4). They are mentioned here, because they include some of the same note classes and types as song bouts. They consist of loud barks and booms, but bitonal screams and long barks or great calls are completely absent, and ululating screams and ascending booms are rare. Mates show little coordination of their vocalisations other than tending to utter bursts of short fast or short slow barks together. A grunting sequence may precede alarm call bouts, but otherwise, no clear sequential structure was recognised.

Similar to song bouts, alarm call bouts have a duration of several minutes and appear to stimulate neighbouring groups to respond in kind. In Studen and Zürich, alarm call bouts occurred infrequently. An eliciting stimulus could not always be discerned by the author. In Zürich, several alarm call bouts of the male *Bh* were apparently triggered by distress calls uttered by a hand-reared siamang infant (*Fa*), when it was left alone in the same building during lunch time.

CHIVERS (1974, p. 242) reported call bouts of wild siamangs in situations of real or potential danger to differ from typical song bouts. He was unable to determine the source of alarm, but suggested that it was likely to be a large cat, raptorial bird, or a snake. Similar contexts were also reported to elicit special alarm call bouts in other gibbon species (CARPENTER, 1940; ELLEFSON, 1974; KAPPELER, 1984; RAEMAEKERS et al., 1984; TENAZA and TILSON, 1977).

In Studen, where I spent the nights in hearing distance of the siamangs, I heard two alarm call bouts occurring at night (both between 03:00 and 04:00). According to the caretakers, these songs may have been produced as an alarm response to rats which I repeatedly observed scuttling around the siamang outdoor cages in the evening. Both captive and wild siamangs have been reported previously to produce nocturnal call bouts occasionally (BOULENGER, 1927; CHIVERS, 1974; HAGEN, 1890; VOLZ, 1903). HAGEN (1890) already stated explicitly that these calls differed from the morning songs. According to local people, these calls were alarm reactions to big animals or predators roaming around in the forest at night.

Because alarm call bouts and song bouts share some note types, they may have a common origin. At least one diurnal alarm call bout in Studen, during which all three resident groups participated, finally graded into a duet song bout. A "relatedness" between alarm calling and singing behaviour was also suggested for *H. lar* and *H. moloch* (CARPENTER, 1940; KAPPELER, 1984), but not for *H. klossii* (TENAZA and TILSON, 1977).

4. Discussion

Of the nine note types described in the present study (Figure 1), only two are sex-specific in the typical duet song of adult siamangs: long barks are typically produced by females, and bitonal screams by males. Speaking in terms of phrases, great calls are produced by females, bitonal scream phrase and US-I phrases by males. The ululating scream and the ascending boom have been described as male-specific vocalisations in most previous reports (FOX, 1977; HAIMOFF, 1981; LAMPRECHT, 1970), but both are regularly produced by some females, albeit not by all individuals. It is unknown why some females only use these vocalisations.

Compared with duets of other gibbon species (e.g. GEISSMANN, 1993, 1995; HAIMOFF, 1983a, 1984; MARSHALL and MARSHALL, 1976), siamang duets exhibit an extremely complex vocal structure. This complexity is manifest in the richness of the partly sex-specific repertoire, in the complicated rules which regulate how notes are combined to exactly timed phrases, and these, on their own, to longer sequences, in the number of points during which mates vocally interact in each great call sequence, and in the strict rules which regulate the sequence of, and the intervals between, these vocal interactions. According to MARSHALL and SUGARDJITO (1986, p. 155) "the [siamang] duet is probably the most complicated opus sung by a land vertebrate other than man." The present study reveals that the organisation of siamang duets is even more complex than previously assumed. The occurrence of a grunting sequence as a regular feature at the beginning of a siamang song bout is recognised here for the first time. No corresponding sequence has been described in songs of other gibbon species.

Most mated siamang males produce an ululating scream both at the beginning and at the end of the great call sequence (see Figures 4 and 5). This recurring pattern of the siamang song structure has not been documented before. The two ululating screams appear to be so closely connected to the great call sequence that they are considered a part of this sequence here.If the two additional ululating screams are recognised as parts of the great call sequence, this would make the sequence even more specialised in siamangs than in other gibbon species. As an alternative interpretation, these screams could be recognised as part of the interlude sequences (which alternate with the great call sequences). But even then, this finding still considerably expands our knowledge of the set of rules which govern the sequential organisation of the siamang duet.

The functions which have been most frequently suggested for duet songs of gibbons are: (1.) Territorial advertisement, (2.) strengthening of pair- or family bonds, or (3.) both (e.g. GEISSMANN, 1999; GEISSMANN & ORGELDINGER, in press). LAMPRECHT (1970) suggested that siamang songs serve multiple functions. MARSHALL and MARSHALL (1976) proposed that different selection pressures act on male and female repertoires in gibbon duets. Possibly, different parts of the same individual's duet contribution may also differ in function (GOUSTARD, 1985), as has been demonstrated for duets in birds (SONNENSCHEIN and REYER, 1983).

As mentioned above, there are considerable differences among gibbon species in the complexity of the song structure and the interaction rules, ranging from species which produce solo songs only (e.g. *H. klossii*), species with a relatively simple duet structure (e.g. *H. leucogenys*), to the siamang with its highly complex vocal interactions. These differences may indicate that song bouts among gibbon species also differ in their functions or in the importance of these various functions (GEISSMANN, 1999; GEISSMANN & ORGELDINGER, in press). Future studies on the function of gibbon songs should, therefore, not approach the songs like an invariable, gibbon-specific feature, because results on one species may not necessarily apply to all gibbon species.

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